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Research Document 2003/073 | **Document de recherche 2003/073**

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Using density-fish size relationships to predict the habitat area of species-at-risk in the Great Lakes.

Utilisation des rapports entre la densité de poissons et leur taille pour prévoir l'aire d'habitat d'espèces en péril dans les Grands Lacs.

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ISSN 1499-3848
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Abstract

Fish catch in numbers per transect was negatively correlated with average fish size in samples from different habitats in near shore areas of the Great Lakes. Density-fish size relationships for the whole fish assemblage and for individual species indicated regression slopes that were not significantly different from –0.9, consistent with the energetics-equivalence hypothesis, but the elevations were habitat dependent. For example, the average density of *Perca flavescens* and *Lepomis gibbosus*, adjusted for fish size, was about two times higher at coastal wetlands than at harbours. The inverse of the density-fish size relationship can be used to estimate the area per fish in each of the habitats. A preliminary predicative equation was: $\log_e$Area = 0.29 + 1.02$\log_e W_{mat}$ + 0.69Capacity, where Area was the area per fish (m^2), W_{mat} was weight-at-maturity (g), and Capacity was a habitat capacity factor (1 for moderate and 0 for good habitat). Based on this equation, the area needed for a hypothetical species that matures at 50 g, assuming a population size of 7,000 fish and assuming good habitat capacity, was calculated to be about 78 ha. To make the predictive model broadly applicable, more research is needed to quantify the use of different habitats at different life history stages.

Résumé

Une corrélation négative a été observée entre le nombre de poissons capturés par transect et la taille moyenne des poissons dans des échantillons prélevés dans différents habitats des zones côtières des Grands Lacs. Le rapport entre la densité et la taille des poissons pour l'assemblage de poissons dans son ensemble et pour chaque espèce a montré des pentes de régression qui ne différaient pas de façon significative de –0,9, ce qui est conforme à l'hypothèse d'équivalence énergétique, mais les élévations dépendaient de l'habitat. Par exemple, la densité moyenne de *Perca flavescens* et de *Lepomis gibbosus*, rajustée pour la taille des poissons, était près de deux fois plus élevée dans les milieux humides côtiers que dans les ports. L'inverse de la relation densité–taille du poisson peut être utilisé pour évaluer la superficie par poisson dans chaque habitat. Une équation préliminaire de prévision se lisait comme suit : $\log_e$ superficie = 0,29 + 1.02$\log_e W_{mat}$ + 0,69 capacité, où la superficie était la superficie par poisson (m^2), W_{mat} était le poids à maturité (g), et la capacité, un facteur de capacité de l'habitat (1 pour un habitat modéré et 0 pour un bon habit). D'après cette équation, on a calculé que la superficie requise pour une espèce hypothétique qui atteint la maturité à 50 g, en supposant un effectif de 7 000 poissons et une bonne capacité d'habitat, était de 78 hectares. Pour que le modèle de prévision soit applicable en général, d'autres recherches sont nécessaires pour mesurer l'utilisation des différents habitats à différents stades du cycle biologique.

Introduction

Conservation programs for fish populations in danger of extirpation require that a habitat area be identified for protection, to not only conserve the residual population but also to provide the space needed for growth towards long-term population viability. A method is proposed (Minns 2003) whereby the area per fish is predicted from the inverse relationship between fish size and fish density. The product of the area per fish and the minimum viable population number can be used to estimate the minimum habitat area that needs to be preserved. Spatial information on the occurrence of the endangered species can be used to determine the geographic boundaries of the protected area.

Animal abundance (D) decreases inversely with adult size as determined by the allometric relationship $D = a\ W^{b}$ (or $\log_e D = \log_e a - b\log_e W$) where the allometric coefficient ($-b$) approximates - 0.75 to -1.0, and the scaling constant a depends on the taxa, population and region (Peters 1983; Peters and Wassenber 1983; Cyr et al. 1997). That is, animal density per unit area decreases in a predictable manner with increases in animal size. For fish assemblages in freshwater, Randall et al. (1995) found that the allometric coefficient was –0.96, and the scaling constant depended on the habitat (river versus lake). In the Great Lakes, the density body-size allometric relationship was evident in electrofishing catch data (but with a lower slope), and also suggested that the intercept was habitat dependent (Randall et al. 1996). Residual variance in the allometric relationship was often high (Peters and Wassenber 1983), and Randall et al. (1995) noted that fish size was an inexact predictor of fish abundance. Nevertheless, area per fish can be estimated roughly from the inverse of the density body-size relationships (Peters 1983; Grant and Kramer 1990; Bohlin et al. 1994; Minns 1995 and 2003).

The hypothesis that the density body-size model is sufficiently accurate to calculate the area requirements of species-at-risk was tested in this study using fish data from littoral habitats of the lower Great Lakes. The specific objectives were to: 1) test if the slope in the allometric relationship between fish size and fish density was different from –0.9 for both individual species and for the fish assemblage; 2) determine if the scaling coefficient (elevation) was habitat-dependent; and 3) determine the precision of an ANCOVA model to predict area per fish based on habitat type (capacity factor) and fish size (covariate). We demonstrate the efficacy of the ANCOVA model for estimating the area requirements of species-at-risk in the Great Lakes and elsewhere. The product of area per fish and viable population number can be viewed as the default value of the habitat area needed by the endangered species to achieve viability.

Methods

Fish catches from electrofishing surveys in the lower Great Lakes were used to test and demonstrate the ANCOVA predictive model. Survey methods for collecting the data are described by Randall and Minns (2002). Briefly, fish surveys were conducted during 1994 in Lake Ontario and Lake Erie at six different locations that included three habitat types in each lake, coastal wetlands, harbour breakwalls, and exposed shorelines (habitat descriptions in Table 1). The total number of line transects was 63, with 30 in Lake Erie and 33 in Lake Ontario. Data from the different habitats could be used to test if the density body-size model for both assemblages and individual species was habitat-dependent.

Fish catches were obtained by electrofishing at the line transects from May to October. Each of 63 transects was surveyed on 3 dates, providing spring, summer and fall samples of fish abundance for each habitat type. Electrofishing surveys were conducted using a 6.1 m boat at the 1.5 m depth contour along 100 m transects that ran parallel to the shore. The generator produced pulsed direct current of about 8 amperes at 120 pulses per second. Information was recorded on species richness (number of species per transect), and the number of fish and total biomass (g wet

weight) per species and per transect. For each sample, fork length (mm) and wet weight (g) of each fish was recorded for catches up to 20 fish per species. If the catch at a transect exceeded 20 individuals for a species, the remaining fish were weighed in a batch, and the total weight and number in the batch were recorded. Average fish weight (g), of the total fish assemblage or individual species per transect, was calculated as total biomass of the 3 combined samples divided by the total number of fish caught.

Fish catch per unit effort data were converted to fish density by assuming a catch efficiency of 0.3 and an effective survey width of 10 metres (Randall et al. 1993). Transect samples with an average fish size less than 20 g were excluded from the calculation of the density fish-size relationship. In a separate study using the same gear, catch-at-age curves showed that small fish of *Perca flavescens* and *Lepomis gibbosus* (< age 2) were captured less frequently in relation to their abundance than larger fish (Randall, pers. obs.).

Analysis of covariance (ANCOVA) models were used to test if the density body-weight models were similar in the different habitats. Both total fish assemblage density and individual species density were used as dependent variables. The expectation was that the area per fish was greater for individual fish species than for fish assemblages, but quantification at both the species and assemblage levels are relevant to determining habitat needs. For individual species, catches of yellow perch (*Perca flavescens*) and pumpkinseed sunfish (*Lepomis gibbosus*) were used, as these species were ubiquitous and were the most abundant inshore species captured in the study (Randall and Minns 2002). Habitat type was used as the categorical predictor and average fish size was the covariate in the ANCOVA models. For each dependent variable, the analysis started with an interaction term (habitat*size) in the model to test for slope differences between habitats. If the interaction term was not significant, an ANCOVA model without interaction was used. Interaction, slope and elevation terms were considered significant at $\alpha < 0.05$. The density-fish size relationship for fish catches in the near shore zone of the Great Lakes was compared to the generalized fish density-size regression for lakes ($\log_e$ density = 10.16 – 0.96 $\log_e$ W; Randall et al 1995).

Area per fish was estimated by inverting the density-weight relationships (Minns 1995; Minns 2003). A correction factor was used to account for the re-transformation bias: $CF=\exp(SEE^2)/2$, where SEE was the standard error of estimate of the regression (Sprugel 1983).

Results

Fish assemblage: There was a negative relationship between total fish catch in numbers and fish-size for the littoral fish assemblage in the different habitat areas (Fig. 1). No fish were captured at one transect in Lake Erie, and the average size of fish was less than 20 g at four shore transects, so the total sample size for the remaining analysis was 58 transect samples. Assuming a catch efficiency of 0.3, average fish density was calculated as 1147 fish ha^{-1} (range 11 to 7878). The slope of the density fish-size relationship for the pooled data was not significantly different among habitats (ANCOVA $F_{2,52} = 1.65$, $P=0.20$), but the elevations were habitat-dependent ($F_{2,54}=34.1$, $P<0.01$). The common slope was –0.86 (95% CL = -1.11,-0.60; $R^2=0.64$). After adjusting for fish size, calculated densities were intermediate at the coastal wetlands (1X; intercept=10.66), highest at the harbours (2.2 X), and lowest at the shore sites (-3.6X). For any given fish size, average densities of the fish assemblages in the littoral habitat were usually greater than the densities indicated by the generalized density fish-size relationship for lakes (Randall et al. 1995). For example, the assemblage fish density in coastal wetlands were about 1.7 times higher than the density in whole lakes (Fig. 1).

Individual species: Densities of *Perca flavescens* and *Lepomis gibbosus* at most transects were less than the generalized density fish-size regression for whole fish assemblages in lakes (Fig 2). Slopes of the density fish-size relationship were not significantly different between species; the common slope was –1.02 (-1.56, -0.47). When the data for both species were pooled, analysis of

covariance indicated that intercepts of the relationship did not differ between species, but fish density was habitat dependent ($F_{2,59}$ = 26.89, P<0.01, R^2=0.48; Fig. 2). The predictive equation was: $\log_e$ density (number per ha) = 8.92 –1.02$\log_e$W (g) –0.69Capacity, where Capacity is a dummy variable for habitat productive capacity (wetland=0, harbour=1). Densities of fish were about two times higher in good habitat (wetland) than in moderate habitat (harbour).

Area per fish was calculated using this density-fish size regression recalculated using the inverse of density (Fig 2, lower). The equation was: $\log_e$ area per fish (m^2) = 0.29 + 1.02$\log_e$W + 0.69Capacity (standard error of estimate = 0.94).

If average fish size is unknown, weight-at-maturity can be used in the equation. Weight-at-maturity for species in the Great Lakes was correlated with average fish size in samples from the field (Fig. 3). Assuming a hypothetical species that matures at about 50 g, a viable population size of 7000 fish (Reed et al. 2003), and habitat with high productive capacity, the critical habitat area was estimated to be about 78 ha (Table 2).

Discussion

Density fish-size models can be used in the Great Lakes to estimate the average area per fish with sufficient precision for the management of species-at-risk. If the minimum viable population size is known or assumed, the minimum habitat area needed to support the population can be calculated as the product of area per fish and population size. In the absence of detailed information on life-stage specific habitat, minimum habitat area is the default estimate of habitat area requirements for recovery plans for endangered species. Minimum area requirements are species (size-at-maturity) and habitat dependent, but knowledge of both predictors is available from the literature. Weight-at-maturity is known or can be estimated for most species of teleosts (Froese and Pauly 1998; Froese and Binohlan 2000). Distribution and preferred habitats if known are described in COSEWIC reports on endangered species (McAllister et al. 1985).

Field data from inshore areas of the Great Lakes confirmed that fish density decreased as fish size increased in the littoral areas. For individual species and for the whole fish assemblage, the slopes of the density-fish size relationships were –1.02 and –0.86, respectively, and were not significantly different. Neither slope was significantly different from the slope of –0.9 as predicted by the 'energetic equivalence hypothesis'. This hypothesis is based on the argument that because metabolic rate tends to scale allometrically with fish weight (Peters 1983), the area required by fish to maintain its metabolic requirements will be proportional to W^b (Bohlin et al. 1994). For fishes, *b* was estimated to be about 0.9 (data cited in Bohlin et al. 1994). The allometric coefficients calculated in this study were consistent with density- and size-related population energetics.

Despite similar slopes, the elevation of the density fish-size relationship depended on both the dependent fish and the independent habitat capacity factors that were used in the ANCOVA models. The average density of individual species adjusted for fish size was considerably lower (about 6 times) than for the whole assemblage. For calculating the area per fish requirements of endangered species, individual species models are more appropriate than assemblage models, as intercepts of the density fish-size relationship for the whole fish assemblage (e.g., Randall et al. 1995) would significantly overestimate density and thus underestimate the area requirements of a single species. For a preliminary species model, data for two abundant species, yellow perch and pumpkinseed sunfish, were pooled because the allometric slopes and intercepts were not different for these two species. Intercepts were also dependent on habitat type, consistent with earlier studies in the Great Lakes (Randall et al. 1996) and elsewhere (Randall et al. 1995). In the Great Lakes, the number of habitat types that can be identified with different capacities is limited (Randall et al. 1998), and a simple two-level predictor (moderate or high capacity) will usually be appropriate. Minimum habitat area to maintain population viability will be greater by a factor of two if habitat capacity is moderate rather than high. Areas where catches of a species are known to be marginal (e.g., shore habitats without structure for pumpkinseeds and perch) should be excluded from the estimate of minimum habitat area.

Comparison of the intercepts of the Great Lakes' field data with intercepts from the general lake regression (dotted line in figures, based on a regression from Randall et al. 1995) assumes that the catch efficiency for calculating absolute density was correct. This was unlikely true, as both the assumed catch efficiency (0.3) and the effective survey width (10 m) were uncertain. For a marked narrow survey swath of 3 metres, Casselman and Grant (1998) visually estimated their catch efficiency at 0.5 and 0.7 for pumpkinseeds and perch, respectively, both higher than the efficiency assumed in this study. In contrast, Bayley and Austen (2002) estimated capture efficiencies that were much lower (0.0018 to 0.14), but their surveys were conducted during daytime, the survey swath was wide (average 13 metres), and they used a different electrofishing boat. Our assumed catch efficiency was probably an overestimate, and if so, the fish densities were underestimated. For the total fish assemblage, the average density from this study was higher than predicted by the Randall et al. (1995) lake regression but this was expected, as the Great Lakes data were from inshore areas while the general regression was averaged for the whole area of inland lakes. Densities of fish in littoral areas are often higher than densities offshore. The magnitude of the difference in fish density between the inshore and whole-lake estimates (1.7 times higher in inshore areas) was probably an underestimate.

In the inshore areas, fish size was an imprecise predictor of fish abundance. The residual variance in the allometric relationships was high; the coefficient of determination for the model was 0.48, and consequently the confidence interval for estimates of area per fish are wide. High variance in this relationship has been observed previously (Peters 1983; Peters and Wassenberg 1983; Randall et al. 1995). The large variance also resulted in a large correction factor to account for the re-transformation bias, adding to the uncertainty of the area estimates. Nevertheless, the allometric density-fish size model is well founded in the literature (Peters 1983) and it provides a quantitative method for calculating the minimum habitat requirements of fish species. In view of the uncertain catch efficiency and the high residual variance, and adopting a precautionary approach, the upper 95% confidence limit could be used in recovery plans to ensure that sufficient habitat area is conserved.

The area-fish size model is presented as a potential method for estimated the area requirements of fish in littoral areas of the Great Lakes, but it is preliminary and has limitations pending further work. The estimate of area is based on fish greater than 20 g in size; area requirements of young fish must also be considered, including migration corridors if different habitats are used for spawning and early growth. Use of the allometric formula for estimating the area requirements of fish smaller or larger than the range in size from this field sample must be tested. Habitat use and species distribution can also change with changes in population abundance (Randall et al. 2003), possibly affecting the density-fish size relationship. The generic allometric formula would be used only as a first order and tentative estimate of area requirements if specific data for the target species were not available.

Density-animal size relationships can be used for other habitats and other endangered taxa as well, such as marine fish, mammals and invertebrates. Peters and Wassenberg (1983) showed that the relationship applies to all taxonomic groups. To be more broadly applicable, more research is needed on density-animal size relationships in a variety of habitats, and on quantitative habitat needs during different life history stages for all species. Quantitative measures of habitat requirements of fish at different ages and size will be a research priority in the Great Lakes. These preliminary observations on the discernible density-size relationship for fishes in littoral areas indicate that the allometric method for estimating area requirements has merit, and further research is warranted.

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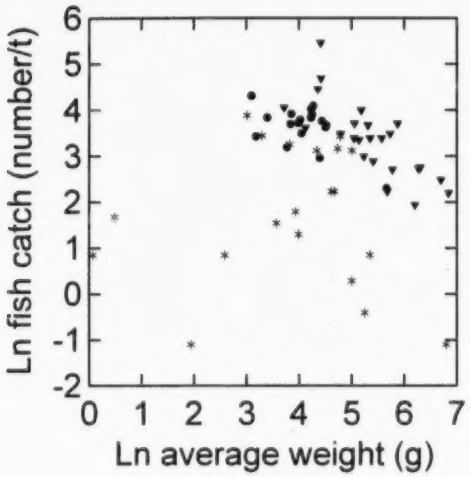
Table 1. Location, habitat type and description, and range in catches of fish from the lower Great Lakes. n is the number of 100 m transects at each location (each transect was surveyed on 3 dates). Specific locations and additional information are provided by Randall and Minns (2002).

Location and habitat type	N	Habitat description	Median catch (range)
Lake Erie			
Coastal wetland	9	fine substrate, abundant macrophytes, moderate wind exposure	44 (10-74)
Harbour	12	armor stone breakwall, nil to sparse macrophytes, variable exposure	24 (7-41)
Shore	9	variable substrate, nil macrophytes, high exposure	2 (0-5)
Lake Ontario			
Coastal wetland	9	fine substrate, abundant macrophytes, low wind exposure	39 (19-60)
Harbour	12	armor stone breakwall, nil to sparse macrophytes, variable exposure	39 (9-236)
Shore	12	variable substrate, nil macrophytes, high exposure	23 (1-49)

Table 2. Calculated minimum habitat area for a hypothetical species with an assumed weight-at-maturity (W_{mat}) of 50 g and a hypothetical viable population size of 7000 fish. Area per fish was calculated using the equation: $\log_e$ area per fish (in square metres) = 0.29 $+1.02\log_e W + 0.69$Capacity (R^2=0.48; standard error of estimate = 0.94). Capacity was 0 for good habitat and 1 for moderate habitat.

Habitat capacity	Area per fish (m^2)[1]	Minimum area of habitat (ha)
good	111	77.7
moderate	222	155.4

[1] a correction factor (1.56) was used to calculate area per fish to account for the bias in log-transformed allometric equations (see Methods).



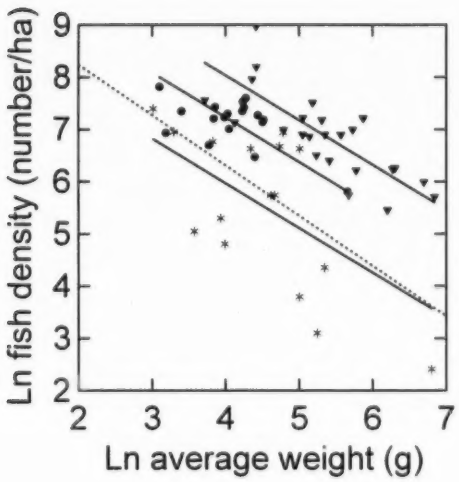
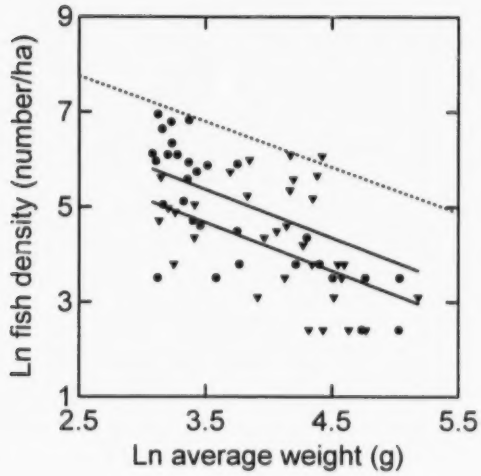


Figure 1. Upper: Relationship between average fish catch (number per transect) and fish size (g). Lower: Calculated fish density (no. ha^{-1}) versus fish size (samples with size < 20 g are excluded). Habitat types were harbours (triangles), coastal wetlands (circles) and shores (asterisks). Solid lines are based on the common slope model with different intercepts for each habitat type (see text). Dashed line is the general density fish-size relationship for lakes from Randall et al. (1995).



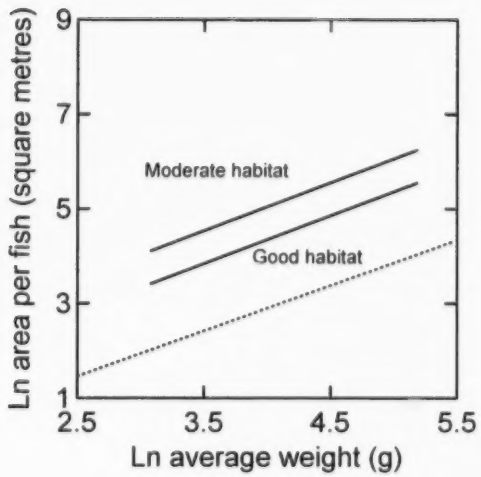


Figure 2. Upper: Density-fish size relationship for *Perca flavescens* (circles) and *Lepomis gibbosus* (triangles). Solid regression lines are for the two habitat types (upper, wetlands; lower, harbours). Lower: Increase in area per fish with increase in fish size for good and moderate habitat. The dotted line in each figure is the generalized regression line for fish assemblages in lakes (Randall et al. 1995).

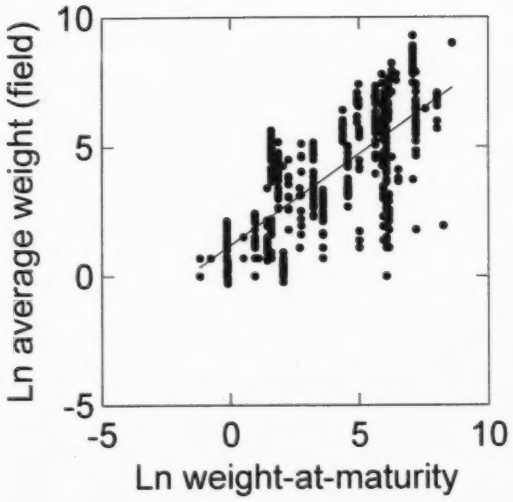


Figure 3. Scatterplot of weight-at-maturity (W_{mat} from Randall and Minns 2000) versus average fish weight (g) in the field samples. Each vertical line of points illustrates the variability in mean size among samples for a species, identified by its literature-based constant W_{mat} on the abscissa. Despite this variability, the literature W_{mat} predicts the central tendancy in mean size for many species. The scatterplot includes data for 34 species.